THE EFFECTS OF ENVIRONMENT ON ANIMALS[1]

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As Henderson[2] has pointed out, the environment on the surface of the earth is suited to, and largely responsible for, the existence of living organisms. After an organism comes into existence, it strives to live in harmony with its immediate environment. An organism is a "system of activities"[3] which devotes its energies primarily to three functions: (1) capturing energy for and releasing energy from its own system, (2) protecting its system from injury, and (3) producing other systems of activities similar to itself. If possible an organism reacts with its environment in such a way that its system continues to exist and carry on its three primary functions. It is limited in its responses to a particular behavior pattern, inherited from the system from which it came, but in general it reacts in such a way toward its environment that it selects by trial the optimum conditions for its own existence. In other words, an organism generally responds in an adaptive way and selects the best environment that it can. If the behavior patterns of certain systems, similar or dissimilar, are well suited to a particular environment, such systems often are "successful." They may take possession of the environment, perhaps exterminating other systems, and, thus demonstrating their "fitness," constitute what ecologists call a climax formation. Every organism in such a group must remain a system of activities and must make continual physiological adjustments to keep in harmony with the environment, or it can not continue to exist. Each organism assumes a

[1] An address before the Geographical Society, University of Wisconsin, January 11, 1922.

[2] "The Order of Nature," Cambridge, 1917.

[3] This definition is not intended to exclude the possibility that an organism may be more than matter and energy. It may contain an entelechy or something similar, but as yet there is no scientific proof that it does. The limitation, and value, of science is that it must always deal with facts.

particular internal pattern that consists of a graded series of metabolic activities which (*de* Child) is a direct response to stimuli received from the environment.

In responding to environment plants and animals show fundamental similarity. Many plants adjust themselves to their surroundings by assuming the form that best suits them to the particular space in which they happen to take up a sessile life, and many animals secure a place which is suited to their system of activities by moving about until they find it. This difference between plants and animals is largely due to the fact that the former usually are able to subsist on inorganic foods, while the latter require organic substances as a basis for their metabolic activities. However, animals often respond to the environment by assuming a particular growth form, and plants have many motile systems of activities that find favorable environments through active or passive migrations. Being trained as a zoologist and knowing little of the activities of plants, I gladly take the task assigned to me—"to discuss the effects of environment on animals"—but I can not refrain from expressing my opinion, that there is no essential distinction in this connection between the two great kingdoms of life.

Animals are continually active and must continually react with the environment. Alcock[4] said, "the three great exigencies: to find something to eat, to avoid being one's self eaten, and to disseminate one's species, give rise to a perpetual struggle in which the fittest are successful." The environment furnishes matter and energy to maintain the activities of each system and a considerable quantity of both is neccessary. A silkworm during its short life eats food amounting to 86,000 times its own weight at the time of hatching. Animals take the most diverse mateials from the environment and use them to build substance or furnish energy. The clothes moth flourishes on a diet of wool, which consists entirely of keratin. From this almost pure, and to most animals wholly indigestible, pro-

[4] "A Naturalist in Indian Seas." London, 1902.

tein substance the moth makes carbohydrate, fat, and water to supply the needs of its system. The bee moth subsists on bee comb, which contains less than one per cent. of protein and a large amount of rather insoluble wax. Ants not only acquire food from the environment, but give up what they have already swallowed to their fellows, even when they are hungry themselves. In this case the "system" of the colony is more important than that of the individual.

In order to keep their systems of activities intact, animals have adopted many means to escape dangers. There are lurking enemies, physical changes, accidents, insidious parasites to be met or avoided continually. A walking-stick spends nine-tenths of its life in a "perfectly quiescent" state, depending on being overlooked by hungry enemies. A house fly escapes through endless agility. A rotifer avoids drying up by secreting a cyst about itself, and may remain dormant for years. Many animals are able to change the usual rate of their metabolic activities in response to changes in temperature and pass cold periods in a hibernating state.

Animals, before all things, use the means they possess in order to perpetuate their particular systems. New individuals must continually be started on new life cycles and such recreations involve reorganizations of systems, changes in metabolism, and various responses by organisms to the environment. Such qualities as odors, colors, and songs may be very important for the survival of a race. A male moth will migrate a mile or more to find a mate—attracted by her odor. The daily routine of seeking and escaping dangers is often neglected by animals when the survival of their race is concerned. Greedy penguins allow any youngster that comes to feed from their crops. An adult bull seal takes no food from May to August, but devotes all his energies to the defense of his rookery. The male gaff-tops'l catfish takes the eggs from his mate and carries them in his mouth for ninety days—denying himself food in order that his offspring

may survive. The little spider that spins a cocoon under stones guards her treasure with watchful care and, if she is compelled to leave her cocoon, spins a ground line as she runs in order that she may return without delay. A male spider dances, postures, and uses all his arts to secure a mate. As soon as he has mated, Nature usually sacrifices his life to his offspring—for his hard-earned mate devours him if she can.

Thus it is wherever one considers animals. There is adjustment, frequently of a very specialized type, to environment. The wonder of it all is the degree of adaptation that animals show. In speaking of food relations Semper[5] said, "there is scarcely a constituent of the earth's crust, whether on land or in water—not an animal nor a plant, whether living, dead, or even in decomposition—which does not afford nourishment to some living animal." The first more or less self-evident generalization justified by this discussion may be stated as follows: *Animals are adapted to the environment.*

That animals are adapted, probably no one disputes, but there has been much controversy as to the means by which they have become adapted. There appear to be three effects that it is possible for the environment to produce in animals: (1) a direct transformation or modification of the living system of activities, (2) the destruction of systems unsuited to the environment and the "survival of the fittest," and (3) the migration of systems from unfavorable to favorable environments.

Animals are modified by external changes and may even take on different forms to suit different environments. Sponges and corals growing in deep water usually have a branching form; the same species in shallow water form flat, encrusting growths. The brine-shrimp, *Artemia salina,* is a classical instance of an animal that has many forms, and these are rather closely correlated with the salinity of the water in which it lives. Sumner[6] and Shel-

[5] "Animal Life as Affected by the Natural Conditions of Existence," N. Y., 1881.

[6] Bull. U. S. Bureau of Fisheries, 1910.

ford,[7] working independently, have shown that very slight structural differences that distinguish closely related species of amphipods and tiger-beetles are correlated with distinct habitat preferences. The structure and physiology of animals are modified by environment—the structures and activities of the systems are changed. Different species may possess almost identical structures, but show specificities of behavior in relation to environment.

Darwin made much of the struggle for existence among animals, pointing out that many species hold their places on the earth through wide dissemination and selective survival. One who has seen the strangler trees gaining a foothold in the tropical forest, the fiddler crabs fighting to hold a favorable place on an ocean beach, or the oysters in an overplanted area striving to survive, can not doubt that there is such a struggle. More animals are produced than can find a place to exist, and in general those survive that are best suited to the environment that is available.

Animals are not always obliged to adjust themselves to the environment or struggle for a favorable place to live in it. They migrate from situations where their systems can not well carry on activities to some spot where conditions are more propitious. In such migrations animals have very definite relations to the environment. They are limited by their reaction pattern to certain habitats; they must disperse from their "centers of origin" through "highways," and are prohibited from migration into certain regions called "barriers." Barriers are areas where certain environmental factors vary beyond the limit of toleration for a species. A "center of origin" as usually understood by geographers, may be the real place of origin of a species or it may merely represent the locality where the most environmental factors are favorable. In general a uniform environment covering a wide range of territory permits the species suited to such an environment to have a wide geographic range.

[7] *Biol. Bull.*, 1911.

Variable species usually have wider ranges than unvarying, because they can adapt themselves to more environmental variations.

A second generalization is appropriate here: *Animals become adapted to environment by* (1) *transformation,* (2) *selective survival from an overpopulated condition,* (3) *migration from unfavorable to favorable situations.*

It will be profitable now to examine two or three typical associations in order to study animals in action with the environment. If, in this connection, one thinks over the great responses that animals have made to environment in the past, he will probably conclude that the greatest habitat change has been that from water to land. It is generally supposed that life first appeared in water. As a habitat, water has certain inherent advantages—the chief of which is perhaps the slowness with which temperatures change. It also has certain disadvantages, the most important of which are probably the variability of its dissolved gases (the higher the temperature, the less gas can be held in solution) and its general solving power, which makes it a transporting medium for all sorts of substances, some of which are poisonous. All animals require a more or less constant supply of water and of oxygen for metabolic processes. When animals forsook the water for land habitats, they gave up surety of water supply and conditions of reasonable thermal stability. What did they get in return? Apparently nothing but a stable gaseous condition for respiratory needs. The danger of desiccation and the wide variations of temperatures incident to land life were apparently compensated for by this gaseous stability. Yet the attractions of the water have at times led many animals, like the aquatic insects, that had become adjusted to life on land to revert to aquatic habitats. In the past races have doubtless many times become adapted by transformation, selection or migration on account of the advantages or disadvantages of one of two habits.

If one walks along a rocky shore, where the ocean

waves and tides sweep, he may be surprised to find an abundant fauna in the " 'tween-tide " zone. The moving water, teeming with microscopic organisms, brings an abundance of food to those animals that are able to stand the beating of the waves and the alternate submergence and exposure due to the ebb and flow of the tides. A rocky wall along the sea shore is no place for weaklings. One minute the blistering sun bakes the exposed animals; the next, the rising tide has covered them with cold water. The waves beat ceaselessly. The changing seasons bring ice and torrid heat. How are the animals on these rocky shores responding to the environment? Here one finds a variety of hardy species which, though not closely related genetically, have many characteristics in common. There are sponges, anemones, hydroid colonies, barnacles, mussels, snails, small crustaceans, and a few scavenger crabs. These animals for the most part obtain their food by net fishing or by straining water through their bodies. They are mostly attached firmly to the rocks, and thus withstand the violent movements of the food-laden water. The barnacles, sponges, and hydroids are grown fast; the anemones and snails have sucking discs that enable them to adhere firmly; the crustaceans have claws for attachment and hard armor covering their bodies. Some of these animals are small and can easily hide in crevices; some of those of larger size, like crabs, are able to migrate to other habitats during violent storms. If an animal is attacked, it is advantageous for it to be able to receive stimuli with facility from all directions of the compass, and, as would be expected, many of the animals on rock beaches are radially symmetrical. Radial symmetry has marked advantages for sessile animals, but puts a weighty limitation on psychic development. An animal that is able to perceive stimuli equally well, through equally efficient sets of sense organs that are symmetrically disposed about a central axis, is never able to develop its power of paying attention to any considerable degree. Its simple mind, if such an animal may be said to have

a mind, must attend now to a stimulus received from one side, now to that on another. Such vacillation is not conducive to the development of higher types of mental life through the delegation of psychic authority to one nervous center. The rocky ocean shores, then, put a premium on radial symmetry and thus as an environment tend to foster psychically unprogressive animals. The barnacles, that appear to have come from progressive, bilaterally symmetrical ancestors, have become degraded with the taking on of the sessile life and radial symmetry that suits them so well to wave-beaten shores.

The ebb and flow of ocean tides have a pronounced effect on shore animals. Those species that are not able to survive alternating exposure to the desiccating effects of air of varying temperatures and the activity of violently moving water of rather constant temperature can not exist on rocky shores. This fauna must be resistant, and is so. An anemone can be kept out of water for a week—until it looks like a dried raisin; or kept in a tightly corked bottle for ten days, and when replaced in the ocean appear to be perfectly normal in an hour or two. Such an animal will not readily succumb to the exposure between tides or even to the stagnation likely to occur in a beach pool that is cut off from the ocean during a prolonged period of low water. The barnacles and molluscs on rocky shores are protected by heavy calcareous shells. Flattely[8] has suggested that land animals perhaps arose in the past on ocean beaches as a result of the resistance developed during exposure between tides.

As a whole the environment occurring on rock beaches offers abundant food, but hard conditions for life. The fauna is highly adapted to resist the two important environmental factors—moving water and exposure to variable conditions—and in this adaptation the fauna has incidentally but of necessity become unprogressive and devotes most of its activities (1) to feeding rapidly when the opportunity comes, (2) to resisting, (3) to resting.

[8] *Science Progress*, 1921.

One does not imagine such a fauna as developing, even through countless ages, great appreciation of beauty, or of any of the æsthetic qualities of "higher" animals. The adaptations here are to resist the unfavorable in the evironment, and still live.

If a man walks in a tropical forest, he is amazed at the abundance and variety of the life about him. He may see a certain species of tree in one spot and not encounter another like it for a mile. Meanwhile he has seen a hundred other species of trees. What is the striking environmental factor in this forest? It is life itself! The environment is favorable for so many systems of metabolic activity that hundreds of kinds of animals are ready to live in it—if they can find a place. Is there a struggle; is there adaptation? Nowhere on the earth are these responses to environment more striking. Most of the struggles to live in the forest are competitions with other living systems that are trying to continue to exist. And the adaptations are not often for resisting, for eating, for resting. Think of all the animals in the tropical forest—is there one that is radially symmetrical? Here keen senses are at a premium. Life has always depended upon seeing, hearing, feeling better than something else. Lately it has come to depend upon thinking better than something else. And the climax of adaptation in this tropical forest has been the greatest thinker of the ages.

A third generalization appears to be justified: *Each habitat, representing environment, limits the patterns of the systems of activities that may persist from reactions within it. The type of adaptation is set by the environment.*

Environment has a quality that any system of activities that attempts[9] to live in it must respond to. This is its changefulness. The paleontologists say that environment punishes too much adaptation by changing. I think it is proper to say that the chief cause assigned for the

[9] The writer realizes that "attempts" may be interpreted as teleological—and rejoices in the sinfulness of it. If an organism does anything, it strives to keep on existing. As far as it possesses means, it responds to whatever interferes with living.

dying out of extinct types of animals is "over-adaptation," or better "too much specialization." A system of activities, as represented by an organism, can not depend absolutely on another system of activities, as represented by environment. The organism changes and the environment changes too. If the environment continues for a time in a fairly stable condition, an animal may become adapted to it to such a degree that, if the environment then does change, the animal can not respond enough to continue to live. The wood frogs in the United States breed when the water is at freezing temperatures; frogs, belonging to the same genus as the wood frog, that live in Cuba die when the temperature falls below seven degrees. These frogs are adapted to different environments and those in Cuba will be in greater danger of extinction if there is a prolonged cold period.

There is a general tendency among animals to find success during conditions of stability. Certain arthropods left the water and attained stable respiratory conditions and freedom from water-soluble poisons by going on land. Later, certain of these arthropods again gained a thermally stable environment in the water and continued to enjoy a stable gaseous environment by carrying air into the water with them. When any race of animals attains a stable environment, it may become specialized to it. We see a manifestation of the same type in the psychology of man. It is "human nature" to desire stability—to be free from care and worry; to know where one stands.

On the other hand, continual change is a stimulus to progressive response—in fact, one is tempted to say that lack of change is injurious to living organisms and that changes often stimulate living systems to renewed activity. Payne kept fruit flies continuously in the dark; Calkins and Woodruff maintained protozoans on unvarying culture media. All these investigators agreed that lack of variation in the environment was injurious. This raises a dilemma—on one hand animals tend to become highly adapted (or specialized) when the environment is

stable, and on the other hand a changing environment is a stimulus to progressive changes in organisms. A few animals have lived for ages in a stable environment. Thompson cites the brachiopod, Ligula, as a "supreme instance of static racial inertia." However, most animals must live in environments that change. How do these respond?

It is a matter of common knowledge that animal systems of activities can become adapted to changes in the environment, even when such changes constitute new racial experiences. By taking increasing doses of certain poisons at regular intervals animals develop enough immunity to be able to take daily a dose which in the beginning would have been fatal. If a pigeon is fed nothing but meat the lining of its stomach changes its character and the bird's metabolic activities become adapted to an unusual diet. Many other instances of acclimatization to new conditions might be cited.

Every physiographer knows that earth environments change by succession. Land forms erode and water forms fill up with sediment. Physiographic succession brings about a succession of environments, or habitats. These are successively occupied by different groups of plants and animals and there is thus an ecological succession, which is a succession of species or groups of species. Shelford has worked out excellent examples of ecological succession in the streams and ponds along the shore of Lake Michigan. Pioneer species of animals invade habitats soon after they are formed, and as the habitats change the pioneer species are succeeded by others that are adapted to later stages in physiographic succession. Ecologic succession is a succession of species; animals do not change as the environment changes, but die or migrate to more favorable localities. Animals do not appear to have special means for adapting themselves to such changes.

There are other types of succession, however, to which animals show striking adaptation. The types are all rhythmic (seasonal, monthly and daily) and depend pri-

marily upon the motion of the earth and moon. As the earth makes its annual journey around the sun, the animals of temperate and polar regions, and to a less extent those in the tropics, are subjected to seasonal changes in environment. These changes are related chiefly to temperature, available moisture, and food. Animals generally respond to such environmental variations by adjusting appropriate activities to favorable times. In general winter is a season for resting; spring, for mating and propagation; summer, for feeding and growth; and autumn for fructification. Seasonal succession is a succession of stages in life cycles. The seasonal rhythm has a short enough period to permit animals to become adapted to it. Their systems of activities vary to fit the seasons. Every one is familiar with the seasonal migrations of animals. The arctic tern travels from pole to pole, and thus always lives in sunshine. Many animals do not migrate, but pass the winter in a dormant condition. In the tropics animals frequently æstivate during the annual dry season. Now many of these seasonal responses are certainly due to stimuli received from the environment. The little Daphnias, that live in fresh-water habitats the world over, usually have long helmets in summer and short helmets in winter, but long-helmeted forms can be made to produce short-helmeted offspring in summer by keeping them at low temperatures. In this instance the effective stimulus appears to be thermal in nature. But animals are adapted to seasonal succession beyond merely responding as far as they are able to stimuli that come with rhythmic changes without their bodies. The living system apparently has a rhythm of its own that is adapted to the seasons. Smallwood[10] kept a female dogfish (*Amia calva* Linnæus) in an aquarium, practically without food, for twenty months at rather constant temperature. During this time the fish twice took on its bright nuptial coloration. Another instance of similar nature has come to the notice of the writer. A tame spermophile, *Citellus tridecimlineatus* (Mitchill), was kept in a steam-heated

[10] *Biol. Bull.*, 1916.

house for four years. In the autumn of the first year it became very fat and stored a large quantity of food in its burrow. About December 1, it went into its burrow, closed the opening, and remained underground for 119 days. The following autumn the spermophile behaved in a similar way but remained underground for only 28 days. It did not hibernate during the two years following. This animal had an established seasonal metabolic rhythm that was correlated with seasonal environmental changes, but the rhythm had a physiological basis for it persisted when appropriate environmental stimuli were not present.

The rotation of the moon about the earth introduces certain rhythmic variations into the earth environment to which animals respond in adaptive ways. Such responses are of course not due directly to the moon as such, but to effects of the moon's motion on matter belonging to the earth. The famous Palolo worm and various other marine annelids come from their hiding places to spawn only during certain phases of the moon. In these worms the eggs do not ripen except when the moon is new or full; the internal activities respond to outside changes, chiefly referable to tidal variations, and a physiological rhythm is established.

The earth rotates on its axis and thus the animals on its surface are subjected to alternating light and dark. Animals readily respond to this short-period rhythmical change. Every one is familiar with nocturnal and diurnal animals. They are adapted to rhythmical environmental changes to such a degree that they may keep on responding periodically when the environment does not change. Keeble and Gamble[11] have described an interesting shrimp (*Hippolyte varians*) that has day and night color phases. During the day this shrimp matches the background on which it rests with a high degree of accuracy, assuming quite a variety of colors and patterns. At night it turns green, regardless of its background. When kept continuously in light it undergoes rhythmic color changes at about the time periods that correspond to day and night

[11] *Phil. Trans.*, London, 1904.

for two days; and makes similar changes in the absence of light for about a week. There is a physiological rhythm that corresponds to periodic environmental changes.

A fourth generalization must again relate chiefly to adaptation—*Though animals possess considerable power of adjustment to new or changed factors in their environment, they apparently do not usually become adapted as species to physiographic changes, but are eliminated by the variation of factors beyond their limit of toleration. One species or group of species succeeds another during physiographic succession. However, animals do respond in an adaptive way to rhythmical daily, monthly and seasonal successions.* Some animals show adaptive responses to rhythmical environmental changes only once during their life cycle. Salmon, for example, do not migrate up rivers to spawn until they have reached a certain age. *Animals apparently become most specialized, or adapted to particular environments, when conditions are most stable. Even the striking instances of adaptations to rhythms show this tendency of adaptation to attain stability—in this case a regularly changing stability.*

Environmental changes have been important in their effects on the evolution of animals. In this paper it has been shown that living systems of activities are adapted to the environment; that they respond to the environment by transformation, selective survival, or migration; that each habitat limits the patterns of the systems that exist within it; and, that, though adaptation to environment may permit precise adjustment to rhythmical changes extending over considerable periods, and though animals generally become most specialized when conditions are most stable, there is no evidence that living systems are caused to change from one species to another by the transformations of habitats due to physiographic succession. The pattern of evolution is set by environment, but there is little or no evidence that changing environment causes adaptive variations of such a degree that new species are produced. Animals adapt them-

selves to environment by changing their systems of activities, but such responses are apparently limited in extent to the inherent possibilities of variation already within the system. Animals have great powers of adaptation to environment, but are not fundamentlly changed by it. Environment permits evolution and controls its course, but does not appear to cause it. If variations fit environment, they are adaptive; if they do not, systems cease to exist. Environment does not appear to cause variation. The living mechanism still holds the mystery of variation within itself. Until there is conclusive evidence, this one great remaining problem of evolution can not be solved. Yet, notwithstanding this lack of evidence, there are still those who belive the environment does cause evolution—though their only foundation for such belief is what Bergson calls "intuition." Until there is proof, science, if it would be scientific, must keep in mind that these "faithful" believers may be right, and be content to wait, perhaps a hundred thousand years —for evidence.

SUMMARY

1. Animals are systems of activities that are adapted to environment.

2. Animals become adapted to the environment by transformation, selective survival, migration.

3. Each habitat limits the patterns of systems of activities that may result from reactions within it. The type of adaptation is set by the environment.

4. Though animals possess considerable power of adjustment to changes in environment, there is no evidence that they became adapted as species to slow changes due to physiographic succession. They do respond to rhythmical daily, monthly, and seasonal changes in an adaptive way. Animals appear to become most specialized, or adapted to particular environments, when conditions are most stable.

5. Environment permits and directs evolution, but does not appear to cause it by forcing the acquirement of new characters.